BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, SEPTEMBER 30, 1978 VOL. 26, NO. 7

FOSSIL POLLEN AND THE ORIGIN OF CORN

ANCIENT POLLEN FROM DEEP CORES IN MEXICO SHOWS THE ANCESTOR OF CORN TO BE CORN AND NOT ITS RELATIVE, TEOSINTE.

PAUL C. MANGELSDORF,* ELSO S. BARGHOORN,** UMESH C. BANERJEE***

There are currently two main schools of thought on the question of corn's origin: one, a 19th century concept, considers teosinte, corn's closest relative, to be its ancestor; the other, a more recent one, maintains that the ancestor of cultivated corn was a wild corn, now probably extinct.

The teosinte theorists argue that since the majority of cultivated species have extant wild ancestral forms, corn must also have its wild counterpart and does so in teosinte (*1*), a species that is widely distributed in parts of Mexico and Central America and which has, for more than a century, been recognized as corn's closest relative (*2*). This school also relies strongly on certain parts of the cytogenetic evidence (*3*), and this particular evidence is indeed impressive. Corn and teosinte have the same chromosome number, hybridize freely, the hybrids are usually highly fertile, the pairing of the parental chromosomes in the hybrids is virtually complete and — perhaps most important — crossing over between them is

*Fisher Professor of Natural History *Emeritus*, Harvard University, and Lecturer in Botany, University of North Carolina.** Fisher Professor of Natural History, Harvard University.*** Honorary Research Fellow, Botanical Museum, Harvard University.

Botanical Museum Leaflets (USPS 404-990). Published monthly except during July and August by the Botanical Museum, Harvard University, Cambridge, Massachusetts 02138. Subscription: $25.00 a year, net, postpaid. Orders should be directed to Secretary of Publications at the above address. Second-Class Postage Paid at Boston, Massachusetts.

essentially the same as it is in pure corn (*4*). All of these circumstances combine to make the teosinte theory much more plausible than it was in the nineteenth century.

The teosinte school concedes that the archaeological evidence presently available lends little support to the teosinte theory but regards this evidence as being outweighed by the cytogenetic evidence. It suggests that supporting archaeological evidence is lacking because the early stages in teosinte's domestication occurred in open campsites where cultural remains have not been preserved (*5, 7*).

On the question of the fossil pollen discovered in Mexico, the teosinte school is distinctly ambivalent. On the one hand it says that this evidence is not to be taken seriously or the data are confusing and ambiguous and they do not solve the problem of the origin of corn (*5*). On the other hand the school asserts that because of the relevance of the fossil pollen to the validity of the teosinte hypothesis it requires rigorous examination (*6*). That examination results in the rather conflicting conclusions that the fossil pollen is not large enough to be reliably distinguished from teosinte, but is too large to be the pollen of a primitive wild corn (*19, 1, 20*). Finally the school explains the fossil pollen as contamination occurring during the core-sampling operation (*1*).

The corn theorists, including the present authors, agree that cultivated corn undoubtedly had an ancestral form and hold that this was a wild corn, probably now rendered extinct initially because of repeated hybridization with cultivated corn once the practice of agriculture began, and later by the depredations of Old-World grazing animals, horses, cows, burros, sheep and goats introduced by the Spaniards and other colonists. This school sees corn differing from teosinte in numerous genetic, morphological, taxonomic and evolutionary characteristics (*8, 9*), and regards the genetic evidence, considered as a whole, as showing teosinte differing from corn not by a few genes (*1*), but by genes or blocks of genes on virtually all of its chromosomes (*8*). This school regards the archaeological evidence as critical and the paleobotanical evidence involving the fossil pollen as virtually conclusive (*10, 13*).

It is the authenticity of the fossil pollen that we wish especially to consider here. Other kinds of evidence bearing on the problem are treated in detail elsewhere (*8, 9*). Suffice it to say here that contrary to a recently published drawing showing an Indian cultivating teosinte (*11*), there is presently no evidence of any kind, archaeological, ethnological, linguistic, ideographic, pictorial or historical, to show that teosinte was ever cultivated as a crop by the American Indians.

DISCOVERY OF THE FOSSIL POLLEN

The discovery of the fossil pollen in question was the result of meticulous studies of palynological samples from cores taken at the Bellas Artes site in Mexico City in preparation for the construction of Mexico's first skyscraper, a 43-story building. (Fig. 1.) These cores were obtained from Dr. Leonardo

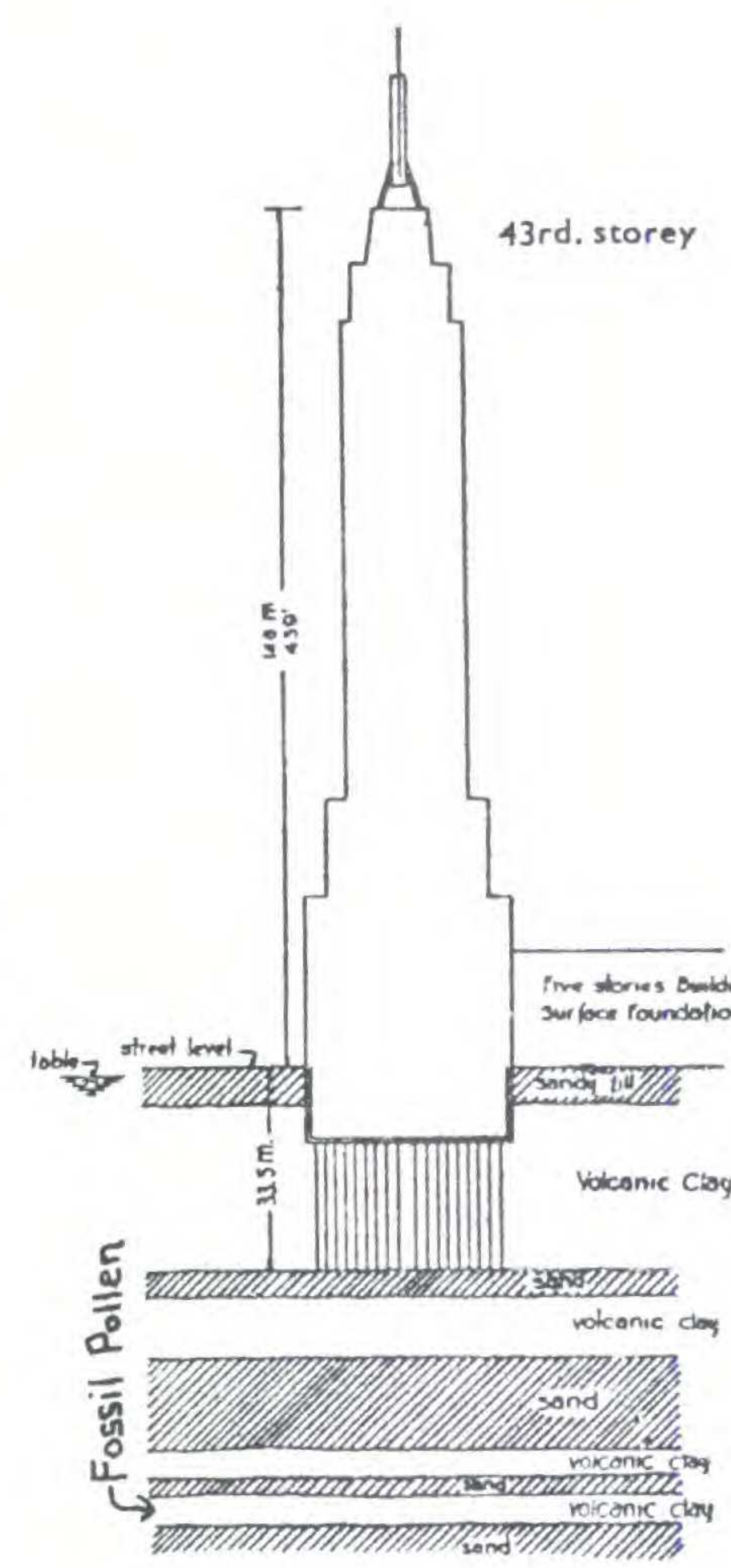

Fig. 1. Fossil pollen, identified as corn pollen, was discovered in core samples taken at depths of 69.3 - 70.5 meters in preparation for Mexico's first skyscraper. An arrow indicates the level of volcanic clay in which the pollen occurred. After Zeevaert (*28*). Depending on the criteria used, this level is variously dated at 25 to 80 thousand years ago. It contains no cultural remains.

Zeevaert, the engineer in charge of the core sampling, by Professor Paul Sears of Yale University for palynological studies to chart climatic changes as they might be revealed by changes in frequencies of pollen of various species especially of pines indicating a drier, cooler period; oak and alder a warmer, moister one and fir a cooler, moister one (*12*). In analyzing the pollen found in the cores, Sears' associate, Mrs. Kathryn Clisby, observed in the lower levels of the profile, 69.3 - 70.5 meters, a number of indubitable grass pollen grains that seemed too large to be identified as those of ordinary grasses. Thinking that these might be the pollen grains of teosinte, Sears and Clisby obtained from Mangelsdorf pollen of several varieties of teosinte. When it became apparent that some of the fossil pollen grains were larger than those of teosinte, Sears, Clisby and Mangelsdorf agreed that these might be pollen grains of corn and decided to send the cores to Elso S. Barghoorn, a paleobotanist at Harvard, for further study. Barghoorn and his then graduate student Margaret Wolfe made an intensive study of the fossil grains, macerating out additional ones from the core centers to eliminate possible surface contamination and comparing them in size and also in the ratio of the pore diameter to the long axis with pollen of fourteen varieties of modern corn, three of teosinte and eight of *Tripsacum*, a more distant relative of corn which, like teosinte, occurs widely in Mexico.

The results of these comparisons show that, although there is an overlapping in size frequencies between the pollen grains of corn and those of teosinte, some of the fossil pollen grains are much too large to be classified as teosinte. We (*13*) concluded that the large fossil pollen grains were almost certainly those of a wild maize once growing in the Valley of Mexico, well before the beginnings of agriculture in Middle America, and this essentially established two important facts:

1. Corn is an American plant and not one of Asiatic origin.
2. The ancestral form of cultivated corn was corn and not teosinte.

The conclusion with respect to corn's American origin seems to have been generally accepted. At least no recent articles arguing for an Asiatic orign of corn have come to our attention.

The second conclusion, that the ancestor of cultivated corn is corn, was also generally accepted, at least for a period, especially when it proved to be quite consistent with archaeological remains of corn, most notably the oldest of these, uncovered by Richard MacNeish in the Tehuacan Valley of Mexico (*14*). Many students of corn thought that the long and sometimes acrimoniously debated problem of the origin of corn had finally been solved.

In the late sixties the old, now long-dormant theory that the ancestor of corn is teosinte was rather suddenly revived. Most prominent in its revival was George Beadle, a Nobel Laureate in Physiology and Medicine and a retired University Chancellor, who, in an interesting personal account, tells his reasons for reviving the theory (*3*).

Beadle was soon joined by others, including Walton Galinat, who believed that the evidence from morphological characteristics which he was then studying outweighed the evidence from fossil pollen or the archaeological remains in which he had participated in describing and publishing (*14, 23*).

The new devotees of the revived teosinte theory were generally not initially deterred by the archaeological evidence which by this time was considerable — or the evidence from the fossil pollen, both of which were neither consistent nor compatible with the concept of corn as a domesticated teosinte. Realizing, however, that the evidence of the fossil pollen was widely accepted by botanists and archaeologists and could not be ignored, they tended to dismiss it by relying on Kurtz *et al.* (*15*). These authors measured pollen from corn plants grown under a variety of environmental conditions, a treatment which resulted in considerable variation in the axis/pore ratio, a measurement which Barghoorn *et al.* had earlier employed as one means of distinguishing the pollen of corn from that of teosinte. Kurtz *et al.* concluded that axis/pore ratio alone is not adequate for making this distinction. The teosinte theory advocates have, with remarkable unanimity, cited or even quoted Kurtz *et al.* as raising serious doubts about the identification of the fossil pollen (*1*, *6*, *16*) but with equal unanimity have overlooked or ignored the statement set forth rather conspicuously in these authors' summary that their data "do not refute the findings of Barghoorn *et al.*" and that five of the fossil pollen grains studied by Barghoorn *et al.* "are sufficiently large in both axis length and pore diameter as well as axis/pore ratio to be classified as maize with a high degree of reliability."

IDENTIFICATION OF THE FOSSIL POLLEN

The problem of identifying the fossil pollen is one of comparing it with the pollen of corn and its two American relatives teosinte and *Tripsacum*. There are no other native grasses with which the fossil pollen might be identified. Distinguishing the fossil pollen from that of *Tripsacum* is not difficult since there is little overlapping in size, only the largest grains of *Tripsacum* being within the range of the smallest grains of corn. Also the pattern of spinules on the exines of *Tripsacum* grains, as revealed by the scanning electron microscope, is quite different from that in corn. In *Tripsacum* the spinules occur in clusters; in corn they are regularly distributed as they are also in teosinte (*17*, *18*).

Since the pollen of corn can not be distinguished from teosinte pollen by their spinule patterns which are quite similar, the only criterion for making a distinction is one of size. It has been asserted that size is not a taxonomic character. This is not strictly true. The principal difference between popcorn and flint corn, for example, is in the size of their kernals. Size of structures is often included as a part of taxonomic descriptions.

In certain instances there is no difficulty in distinguishing corn and teosinte pollen by size alone. For example, in a recent publication (*18*), the photographs of pollen of Guerrero teosinte and Confite Morocho corn show the corn pollen to be only slightly larger than the teosinte pollen. But when the corn pollen is enlarged to the same magnification, x 1692, as the teosinte pollen it proves to be half again as long as the teosinte pollen with about twice the volume.

Although individual grains of corn pollen cannot always, as was possible in this case, be distinguished from individual grains of teosinte, populations of pollen grains can usually be distinguished. A comparison of the frequency distributions of 200 archaeological grains of pollen from the Bat Cave site in New Mexico with 200 grains of pollen from a teosinte growing in the Valley of Mexico shows some overlapping (*19*). In the region of overlap the grains of corn and teosinte cannot be distinguished. But 59 percent of the Bat Cave pollen grains are larger than the largest teosinte grains. Distinguishing these from the teosinte grains is no problem.

The population of the fossil pollen grains from the Bellas Artes site is clearly different from any population of teosinte grains with which it has been compared. There are, as Kurtz *et al.* have stated, at least five pollen grains, 36 percent of the total, too large to be identified as teosinte pollen.

The teosinte theorists now argue that the fossil pollen grains, earlier considered to be too small to be reliably distinguished from teosinte grains, are too large to be those of a primitive corn (*1, 5*). This argument is based on a correlation showing a relationship between length of ear and pollen size (*20*). The length of the ear determines to a considerable extent the length of the styles, commonly called "silks", that the pollen tubes must travel to reach the ovules and effect fertilization.

Since the ears of a primitive wild corn are assumed to have been small, the earliest intact cobs from San Marcos Cave in the Tehuacan Valley vary in length from 19 - 25 mm (*14*), it is concluded that the pollen of such a corn must have been correspondingly small. This does not necessarily follow. Actually the correlation mentioned above, although statistically significant, is strongly influenced by two races, Jala and Huesillo, that have unusually long ears and unusually large pollen. The correlation among the remaining eight races included in the study is by no means so strong and there are notable exceptions. The highly evolved Mexican race Vandeño, for example, has pollen grains of about the same size, 83.9 microns, as those of the primitive Mexican popcorn race Nal-Tel, 81.2 microns, although its ears are more than twice as long as Nal-Tel, 17.2 and 7.9 cm, respectively.

SIGNIFICANCE OF THE LARGE POLLEN

It is the large pollen of the primitive popcorn that seems to us to be especially significant and to require explanation. The length of the mature ear is only one factor in determining the length of the styles that the pollen tubes must travel to reach the ovules. Equally important is the extent to which the husks protrude beyond the tips of the ears which they enclose. The senior author has frequently been impressed by the fact that among the early archaeological remains the husks are considerably longer, on the average, than the longest cobs of the same level. This first came to attention in the archaeological remains turned up in the first Bat Cave expedition. The only husk found in the lower levels of the cave is quite long, 24.5 cm, more than twice the length of the longest intact cob, 10.3 cm. The authors (*21*) concluded that the husk must have been an involucre of leaf sheaths subtending and surrounding the base of an ear but not tightly enclosing it.

The real nature of this long husk became apparent with a study of the specimens from the second Bat Cave expedition (*22*). These led to the conclusion that the long husk found in the first expedition may have enclosed, not a single ear, but a pair of ears, upper and lower, each with its own shorter husk system (Fig. 2). If the silks of the lower ear became exposed to pollination only when they reached the terminus of the outer husk system they would have been about 23 cm long. This is longer than any of the ears in the correlation study reported above except the giant ears of the races Jala and Huesillo, but is about the length of the longest silks of the race Vandeño, when allowance is made for the husks extending several inches beyond the tip of the ear as they do in most varieties. Thus the fact that the highly-evolved race Vandeño has the same pollen size as the primitive popcorn race, Nal-Tel becomes explicable.

The two-eared husk system may also explain the two-ranked, four-rowed cob found in the lower level of San Marcos cave. The teosinte advocates regard this as evidence of the evolution of the early Tehuacan corn from teosinte. A more simple and obvious explanation is that this cob represents a lower secondary ear in a two-eared husk system. Lower sec-

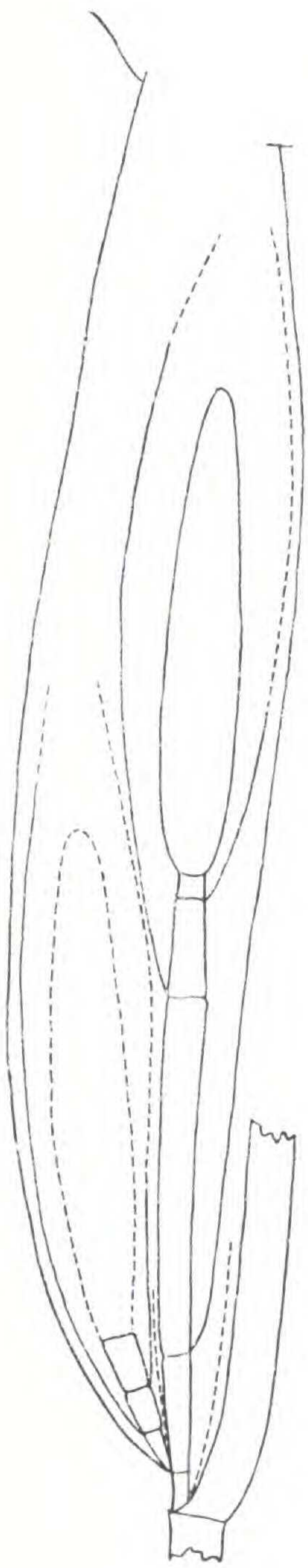

Fig. 2. Archaeological evidence shows that primitive corn may sometimes have borne two ears, an upper and a lower, in the same husk system. To reach the terminal opening of the outer husks the styles — "silks" — attached to the basal ovules of the lower ear would have to be quite long and the pollen grains effecting fertilization quite large. This wild corn may have been "preadapted" to evolve under domestication in the direction of producing long single ears. Teosinte does not have this preadaptation. Solid lines represent actual parts; broken lines artist's reconstruction. Drawn by Julián Cámara-Hernández (*22*). 1/2 actual size.

ondary ears, even in modern corn varieties, are often two-ranked and four-rowed.

Husk systems similar to the one described from Bat Cave and illustrated in Fig. 2, have also been found in the remains from San Marcos Cave in Tehuacan and the Huarmey Site in Peru (*23*, *24*).

Primitive corn as we now conceive of it with its large pollen may thus be recognized as a classic example of what some students of the dynamics of domestication, notably Vavilov and Hawkes (*25*), regard as "preadaptation."* These authors stress the fact that primitive ancestral forms of successul cultivated plants already possessed tendencies which induced man to cultivate them. Corn had its share of these especially in its easily harvested and threshed grain, and its conspicuous response to man's ministrations: freedom from competition with other vegetation and increased soil fertility. Early cultivators, although perhaps noting corn's large pollen grains, just visible to the naked eye, could scarcely have been aware of their significance. But it was its large pollen grains that gave corn the ability to evolve in the direction of producing larger and larger ears. If ever there was a wild species preadapted to domestication, corn is perhaps the prime example of this condition. Teosinte does not have this preadaptation; it could not have evolved in this direction without a series of mutations involving pollen size.

POSSIBILITY OF CONTAMINATION

One recent explanation of the fossil pollen is that it represents contamination (*1*), either from modern pollen at the upper levels being carried to a lower one during the sampling or from pollen in the air when the sampling was being done. To explain the fossil pollen as contamination is, of course, to assume that it is indeed corn pollen.

That pollen in the 1 - 3 meter level could be carried down to the 69.2 - 70.5 meter level leaving no contamination at intervening levels seems quite improbable, if not impossible, in view of the precision of the equipment and the techniques employed in

*Further reading has shown us that the idea of preadaptation as presented by these authors, is new only as it applies to evolution under domestication. Simpson in his book, *Tempo and Mode in Evolution* (Columbia University Press, 1944) discusses at length the concept as it applies to evolution in nature. Students of corn's evolution, including the senior author of the present article, have perhaps been remiss in not recognizing the phenomenon of preadaptation as an important factor in corn's amazingly rapid evolution under domestication. Included among corn's preadaptive characteristics is its ability to hybridize and exchange genes with its relatives, teosinte and *Tripsacum*. Teosinte lacks this characteristic, since, if it is cultivated corn's only ancestor, it had no wild corn, *Zea Mays*, with which to hybridize and its does not, even under ideal experimental conditions, hybridize successfully with *Tripsacum*.

the core sampling. The possibility of contamination by atmospheric pollen appears to be equally remote.

The Bellas Artes site is centrally located in greater Mexico City, one of the largest metropolitan areas in this hemisphere. It is many miles removed in all directions from the nearest corn-growing areas. We do not know exactly how far corn pollen can be carried by the wind but compared to the pollen of some other species, pines for example, it is relatively heavy. Agronomists and seed producers maintaining the purity of breeding lots of corn allow about one thousand feet of isolation if the contaminating pollen comes from the windward side, less if physical barriers to air flow are present (*26*). During the time of year that corn pollen would be shedding in Mexico City, if corn were there, the air is relatively still, indeed so much so that industrial pollution not carried away by the wind has become a major problem.

An experiment performed for another purpose by a Harvard graduate student, Ramana Tantravahi, may have a bearing on the question of how far corn pollen can travel with the wind. In order to effect the hybridization of teosinte with *Tripsacum* on a large scale, Tantravahi grew emasculated plants of teosinte adjacent to pollen-shedding plants of *Tripsacum* in a small garden surrounded by University buildings in Cambridge. To test the effectiveness of the emasculation of teosinte and to detect contamination by corn pollen from any source he also grew in the garden a row of emasculated corn plants. When the ears of these were examined at the end of the season, not a single kernal was found (*27*), although there were extensive plantings of corn in the market-gardening area near the Waltham Field Station about six miles due west of Harvard University. The winds during the corn-pollen-shedding season are prevailingly from the west. These observations suggest that corn pollen cannot ordinarily be carried as far as six miles.

The possibility that there was corn pollen in the air at the Bellas Artes site when the soil sampling occurred is quite remote. Almost equally remote is the possibility that such pollen, if actually there, could have contaminated the core samples.

The core sampling at the Bellas Artes site that revealed the fossil pollen is not an ordinary drilling operation involving repeated pouring of water or drilling mud into the hole, thus providing abundant opportunities for contamination. Core sampling in preparation for the construction of a skyscraper is an operation of considerable precision — one that is especially designed to yield undisturbed samples. Essentially it involves a series of tubes driven through the soil at successive levels. As the tubes are removed, they are immediately sealed at both ends with a special wax and are sent to the laboratory for various analyses. Engineers familiar with the problems of soil mechanics who have examined the data in Dr. Zeevaert's article in *Geotechnique* (*28*) describe his operation as "extraordinarily careful and meticulous."

Dr. Zeevaert himself seems quite certain that the cores in which the fossil pollen was found are undisturbed samples. In a letter of October 17, 1973, to Barghoorn, he wrote:

> Indeed the sampling of the material was performed with a special sampler to obtain undisturbed samples of the soil, useful to determine the natural compressibility and sheer strength properties of the materials. Therefore, the samples taken were not disturbed or contaminated, they were 'undisturbed samples' used in soil mechanics to determine the 'in situ' mechanical properties of the materials. Therefore, you can be sure that the investigations made on these samples concerning the fossil maize pollen are reliable.

We are inclined to accept Dr. Zeevaert's statement as factual. We are pleased to note, in passing, that Dr. Zeevaert has recently been elected a foreign member of the United States National Academy of Engineering.

Finally the fossil pollen itself demonstrates that it is not the product of modern contamination. It does so in this way: it is one of the standard palynological techniques to prepare pollen for electron microscope studies by a treatment known as acetolysis (glacial acetic acid and concentrated sulfuric acid, 9:1). This treatment is described in detail by Banerjee (*29*). Suffice it to say here that corn pollen when fresh resembles in shape an inflated basketball; when dry the shape of a deflated ball. Pollen from extant corn plants is restored to its original inflated shape when subjected to the acetolysis treatment (Plate 18A). But the pollen from the Bellas Artes does not respond as does modern pollen to this treatment (Plate 18D). This is true also of certain other ancient pollen. Pollen from Coxcatlan Cave in the Tehuacan Valley dated at *ca.* 1900 years failed to expand completely with the acetolysis treatment (Plate 18C). On the other hand pollen from the same cave at *ca.* 1600 years expanded almost like modern pollen (Plate 18B). Apparently as the chemical constituents of the pollen grains change with age certain of them lose their ability to react with the chemicals introduced by the acetolysis treatment (Plate 18C). What these constituents might be is a question beyond the scope of this discussion. The important point here is to recognize the fact that ancient pollen grains differ from modern ones in their capacity to respond to certain chemical treatments. The loss of this capacity seems to begin at about 2000 years; we do not know at what age it is completely lost. Pollen from the Huarmey site in Peru, dated at 3600-4000 years (*20*) is only slightly more collapsed than the pollen shown in Plate 18C dated at 1900 years (*29*).

The failure of the Bellas Artes pollen to respond to the acetolysis treatment combined with the fact that opportunities for contamination, discussed above, are minimal, if not actually nonexistent, has persuaded us that this pollen is indeed ancient and not the product of modern contamination. Having previously satisfied ourselves that the pollen has been correctly identified as corn pollen, we can now only conclude that the fossil pollen is authentic and if so, it is more than highly probable that the ancestor of cultivated corn was corn and not teosinte.

IMPLICATIONS FOR CORN IMPROVEMENT

Eliminating teosinte as the ancestor of corn does not mean, however, that it has had no role in the evolution of cultivated corn. On the contrary, archaeological remains are consistent in showing that although the earliest corn may have been pure corn, later corn is the product of hybridization with teosinte. And the hybridization still continues (*30*).

To the puzzled onlooker the distinction between recognizing teosinte as *an* ancestor of modern corn while vigorously denying it to be *the* ancestor may seem to be no more than an exercise in semantics. From the standpoint of theoretical genetics and practical plant breeding, however, it is much more than that. If teosinte is *the* ancestor of corn and the only one, then modern corn contains only one stream of germplasm. But if the ultimate ancestor of corn was corn, as the fossil pollen and the archaeological remains show, and modern corn is the product of repeated introgression from teosinte, then two distinct streams are involved and modern corn, although a diploid, has some of the attributes of an allopolyploid (*8*). In this respect it is comparable to the allopolyploid cereals like bread wheat, one of the world's most productive food plants, the product of hybridizing three species, two of which have never been recognized as worthy of cultivation and a third, einkorn, which being generally quite unproductive, is but little grown.

The interactions of these two streams of germplasm, corn's and teosinte's, has produced profound effects, including genetic recombination, heterosis — hybrid vigor — and mutagenesis (*31*). These, combined with corn's preadaptation to changes in ear length, by virtue of its large pollen, have resulted in the explosive evolution (*23*) illustrated in Plate 19. It is doubtful if such rapid evolution could have occurred were teosinte the only ancestor of corn. Then the hybridization of cultivated corn, originating from teosinte, with its ancestor, teosinte would have produced a minimum of genetic recombination and heterosis and probably no mutagenesis, and any increase in ear length would have been inhibited by teosinte's lack of preadaptation because of its small pollen.

To the practical plant breeder the difference in the two theories may determine the most promising methods of employing genes from teosinte. Shall he hybridize corn directly with teosinte or shall he hybridize strains of one race of corn containing teosinte germplasm with strains of another race containing a somewhat different combination of teosinte genes? In both strains the teosinte genes or blocks of genes will have been absorbed into the corn genotype by the natural selection of modifying genes that suppress the undesirable characters of teosinte and allow the desirable ones to be expressed. The genotype of modern corn may well be a constellation on a grand scale of DNA recombinants.

So far little progress in corn breeding has been made by hybridizing corn directly with teosinte but phenomonal results have been obtained by combining strains that are the product of past introgression from teosinte as shown by anatomical and genetic studies (*32*).

The average yields of corn in the United States have increased from 26 bushels per acre in 1929 to 95 bushels in 1972. This progress has involved the bringing together by empirical methods of strains of germplasm from diverse sources, much of it originally from teosinte. There are many races of corn not yet employed in hybrid corn breeding (*33*). Recognizing the potential value of these for breeding opens new possibilities for improvement that may render corn, this nation's basic food plant, still more important on the world scene as one of not more than about twelve species of cultivated plants, each one a unique biological system, that quite literally stand between mankind and starvation.

SUMMARY

Fossil pollen discovered in core samples from a depth of 69.3 - 70.5 meters in preparation for the construction of Mexico's first skyscraper has been identified as the pollen of a primitive wild corn. Its authenticity seems now to be well established since the possibility that the pollen represents modern contamination is shown to be remote. The authors conclude that the ancestor of cultivated corn was a wild corn and not its closest relative, teosinte, and that this may have important implications for corn's genetic improvement and its role in meeting the world food problem.

POSTSCRIPT

Two important events occurred while this paper was in proof. An article by Iltis *et al.* (appearing in *Science*, Jan. 12, 1979) announced the discovery in Mexico of a diploid perennial teosinte. As senior author of the present article, I recognized this as a significant discovery and I wrote Iltis at once congratulating him. I failed, however, to recognize the full significance of the discovery. It remained for H. Garrison Wilkes, the author of the book, *Teosinte: the Closest Relative of Maize* (2), presently in India, to point out in a letter to me, dated Jan. 17, that this discovery may be the key piece in the puzzle, a so-called "missing link" in corn's genealogy. Wilkes assumes, correctly I think, that hybridization between the diploid perennial teosinte and a wild annual corn could have produced all of the known annual races of teosinte. This assumption is to a large extent testable.

I am urging Wilkes to publish this concept and its implications as soon as possible, and I am hoping that this postscript will serve to establish his priority for an imaginative and important new idea. The relevance of our present article to this new concept is obvious.

REFERENCES AND NOTES

1. G.W. Beadle, in *World Anthropology, General Editor Sol Tax Origins of Agriculture*, Charles A. Reed, Ed. (Mouton Publishers, The Hague-Paris, 1977), p. 615; *Ibid.*, in *Report of Thirty-Second Annual Corn and Sorghum Research Conference*, H.D. Loden and D. Wilkinson, Eds. (American Seed Trade Association, Washington, D.C., 1977), p. 1.
2. H.G. Wilkes, *Teosinte: the Closest Relative of Maize*. (Bussey Inst. Harvard Univ., Cambridge, Mass., 1967).
3. G.W. Beadle, *Field Mus. Nat. Hist. Bull.*, 43, 2 (1972).
4. R.A. Emerson and G.W. Beadle, *Zeitsch. Ind. Abstamm. Vererb.*, 62, 305 (1932).
5. W.C. Galinat, in *Corn and Corn Improvement*, G.F. Sprague, Ed. (Amer. Soc. of Agronomy, Madison, Wisconsin, 1977), p. 1.
6. *Ibid., Ann. Rev. Genetics*, 5, 447 (1971).
7. *Ibid.*, in *Genetics and Breeding of Maize*, D.B. Walden, Ed. (Wiley & Sons, New York, 1978), p. 93.
8. P.C. Mangelsdorf, *Corn Its Origin, Evolution, and Improvement*. (Harvard Univ. Press, Cambridge, Mass., 1974).
9. L.F. Randolph, *Econ. Bot.* 30, 321 (1975).
10. P.C. Mangelsdorf, *Field Mus. of Nat. Hist. Bull.*, 44, no. 3, 16, (1973).
11. H.G. Wilkes, *Science*. 200, 41 (1978).
12. K.H. Clisby and P.B. Sears, *Bull. Geo. Soc. Amer.*, 66, 511 (1955); P.B. Sears and K.H. Clisby, *Ibid.*, 521 (1955).

13. E.S. Barghoorn, M.K. Wolfe, K.H. Clisby, *Bot. Mus. Leafl. Harvard Univ.*, 16, 229 (1954); P.C. Mangelsdorf, *Amer. Antiquity*, 19, 409 (1954).
14. P.C. Mangelsdorf, R.S. MacNeish, W.C. Galinat, *Science*, 143, 538 (1964).
15. E.B. Kurtz, J.L. Liverman, H. Tucker, *Bull. Torr. Bot. Club*, 87, 85 (1960).
16. J.M.J. De Wet and J.R. Harlan, *Euphytica*. 21, 27 (1972); T.A. Kato Y., *Cytological Studies of Maize and Teosinte in Relation to their Origin and Evolution*. (Mass. Agric. Exper. Station, Univ. of Mass. Amherst, 1975); J. Schoenwetter, *Amer. Antiquity*. 39, 292 (1974).
17. U.C. Banerjee and E.S. Barghoorn, *30th Ann. Proc. Electron Microscopy Soc. Amer.*, C.J. Arceneaux, Ed. (1972).
18. C.A. Grant, *Grana*. 12, 177 (1972).
19. W.C. Galinat, *Maize Genet. Coop. Newslet.*, 47, 105 (1973).
20. W.C. Galinat, *Maize Genet. Coop. Newslet.*, 35, 39 (1961).
21. P.C. Mangelsdorf and C.E. Smith, Jr., *Bot. Mus. Leafl. Harvard Univ.*, 13, 213 (1949).
22. P.C. Mangelsdorf, H.W. Dick, J. Cámara-Hernández, *Bot. Mus. Leafl. Harvard Univ.*, 22, 1 (1967).
23. P.C. Mangelsdorf, R.S. MacNeish, W.C. Galinat, in *The Prehistory of the Tehuacan Valley: Environment and Subsistence*, D.S. Byers, Ed. (Univ. of Texas Press, Austin & London, 1967), 1, p. 178.
24. A. Grobman, D. Bonavia, D.H. Kelley, P.C. Mangelsdorf, J. Cámara-Hernández, *Bot. Mus. Leafl. Harvard Univ.*, 25, 221 (1977).
25. J.G. Hawkes, in *The Domestication and Exploitation of Plants and Animals*, P.J. Ucko and G.W. Dimbleby, Eds. (Gerald Duckworth & Co., London, 1969), p. 17; N.I. Vavilov, *Bull. Appl. Bot. Pl. - Breed.*, 16, 1 (1926).
26. W.F. Craig, in *Corn and Corn Improvement*, G.F. Sprague, Ed. (*Amer. Soc. of Agronomy*, Madison, Wis., 1977), p. 671.
27. R. Tantravahi, unpublished.
28. L. Zeevaert, *Geotechnique*. 7, 115 (1957).
29. U.C. Banerjee, *Morphology and Fine Structure of the Pollen Grains of Maize and its Relatives*. (Ph.D. Thesis, Harvard Univ., Cambridge, Mass., 1973).
30. H.G. Wilkes, *Econ. Bot.*, 31, 254 (1977).
31. P.C. Mangelsdorf, *Cold Spring Harbor Symp. Quant. Biol.*, 23, 409 (1958).
32. G.S. Johnston, *Manifestations of Teosinte and "Tripsacum" Introgression in Corn Belt Maize*. (Bussey Inst. Harvard Univ., Cambridge, Mass., 1966); P.C. Mangelsdorf, *Euphytica*, 10, 157 (1961); S.M. Sehgal, *Effects of Teosinte and "Tripsacum" Introgression in Maize*. (Bussey Inst. Harvard Univ., Cambridge, Mass., 1963); S.M. Sehgal and W.L. Brown, Econ. Bot., 19, 83 (1965).
33. M.M. Goodman and R. McK. Bird, *Econ. Bot.*, 31, 204 (1977); E.J. Wellhausen, *Ann. Hybrid Corn Industry - Res. Conf. Proc.*, 20, 45 (1965).
34. Our thanks to Major M. Goodman, L.F. Randolph, Robert Bird, Clark P. Mangelsdorf, Paul C. Mangelsdorf, Jr., and Dennis Porter.

PLATE 18

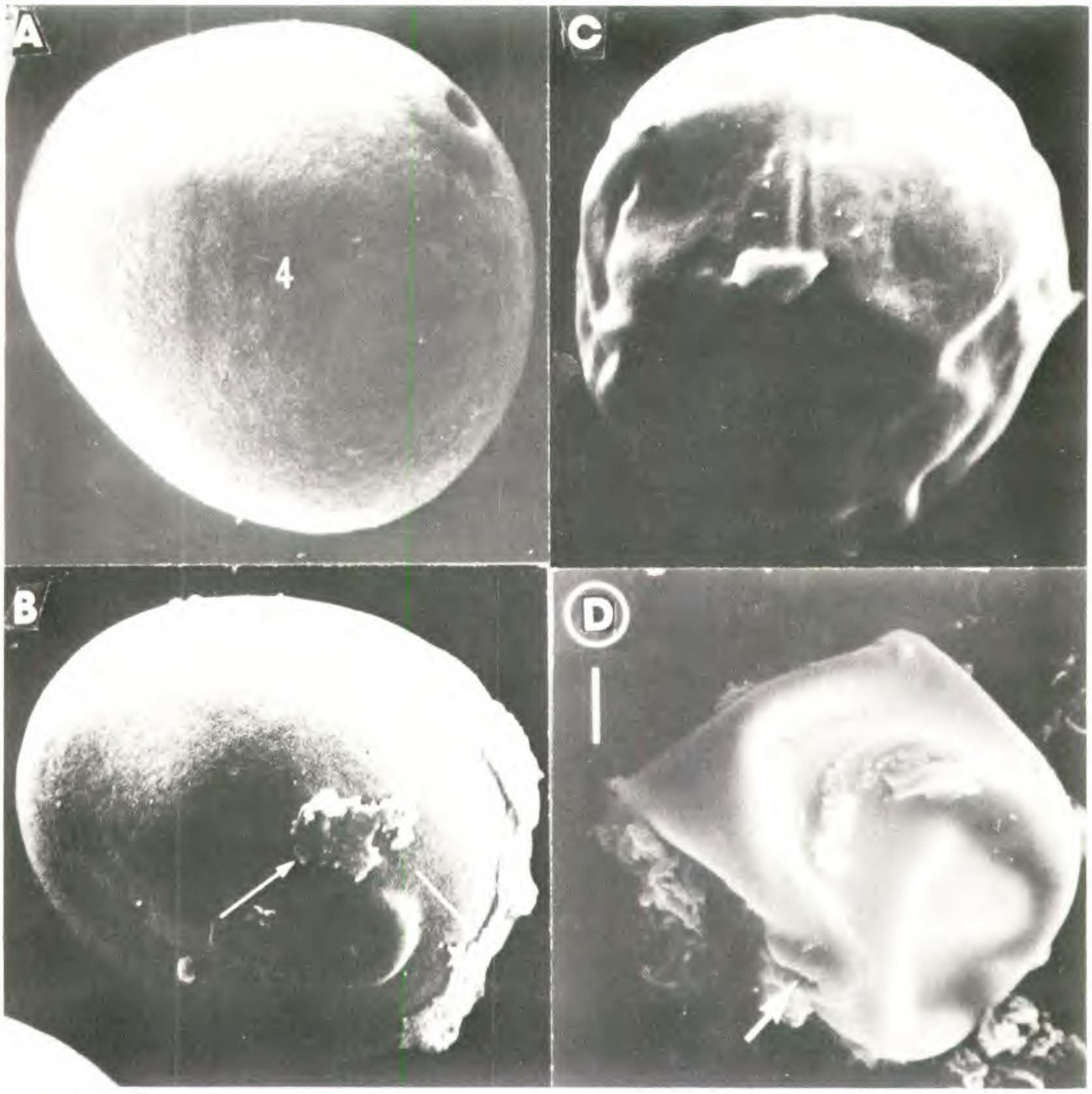

Plate 18. The effect of the acetolysis treatment on restoring pollen to its original shape. A. Modern pollen grain of the Mexican popcorn race Polomero Toluqueño, fully expanded after treatment; B. Archaeological pollen grain from the Tehuacan site, Mexico *ca* 1600 years old, expanded; C. Pollen grain *ca* 1900 years old from the same site, slightly collapsed; D. Fossil pollen grain from the Bellas Artes site, Mexico, completely collapsed, showing that it is ancient and does not represent contamination of the core samples.

PLATE 19

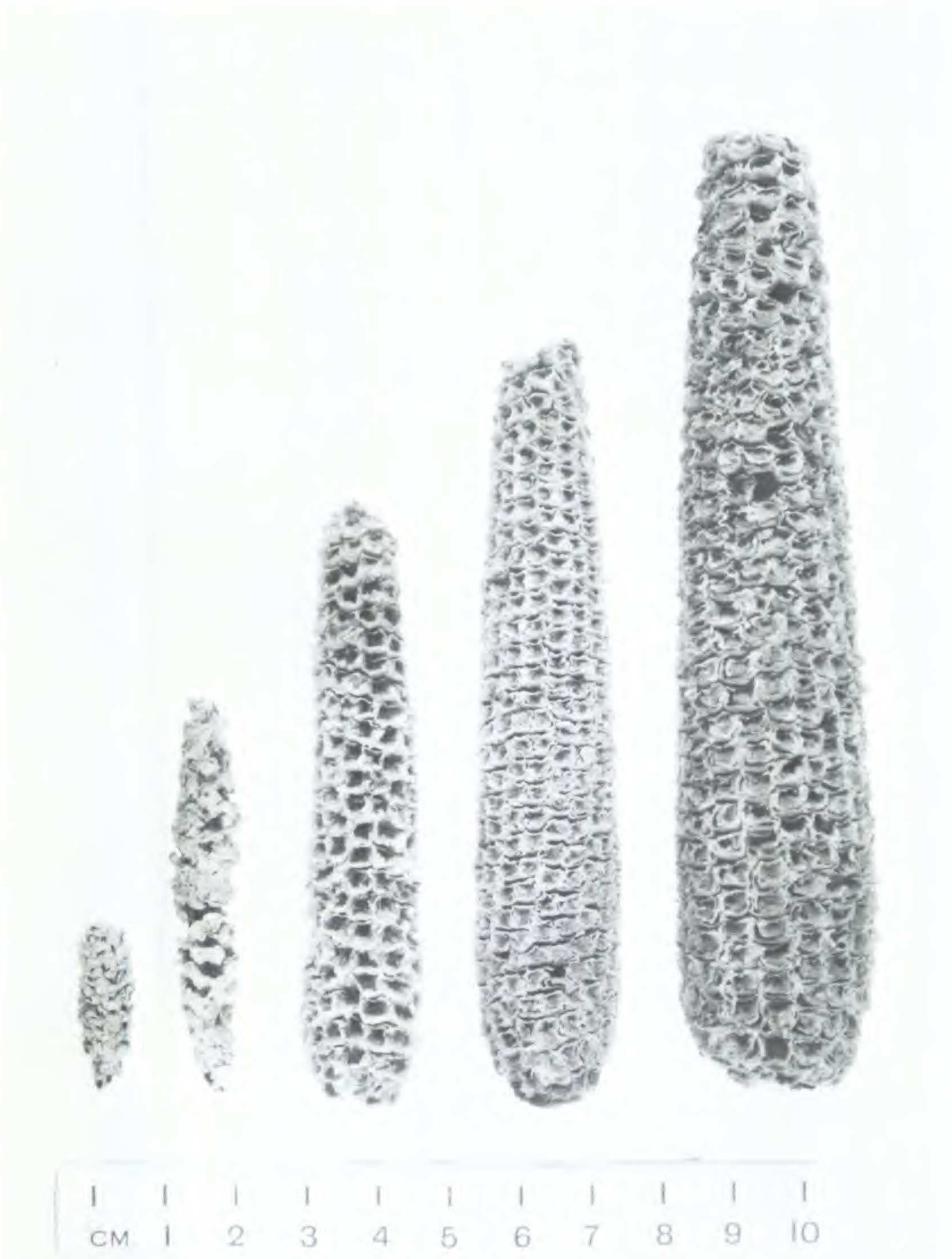

Plate 19. Evolution in ear length in 6500 years in the Tehuacan Valley, Mexico. The approximate ages of the cobs from left to right are 7000, 5300, 2200, 450 and 450 years respectively (*23*). This evolution, rapid as compared to that of other cultivated plants, is partly the product of wild corn's preadaptation to domestication by virtue of its large pollen as revealed by the fossil remains from the Bellas Artes site, Mexico.